Habitat heterogeneity facilitates coexistence of two syntopic species of *Peromyscus* in a temperate forest of Central México

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An essential topic in ecology is to understand how the structure of the habitat and its changes in space and time (*i. e.*, habitat heterogeneity) affect the frequency and interactions between cohabiting species. Here, we assessed the effect of the biotic and abiotic components that configure the microhabitat heterogeneity and its temporal shifts (dry and rainy seasons), on the frequency (total and by sex) of two congeneric species, *Peromyscus difficilis* and *P. melanotis*, that co-occurs in a temperate forest of Central Mexico. To address this, an experimental plot composed of 120 sampling stations was placed within a temperate forest in the National Park Desierto de los Leones, Mexico City. In each sampling station, we set Sherman traps to capture mice of two syntopic *Peromyscus,* and we also evaluated six variables related to the spatial heterogeneity of the habitat during two rainy seasons. Our results revealed differential effects of habitat heterogeneity on the frequency of each species. Moreover, habitat heterogeneity also had a different effect on male and female frequencies of each *Peromyscus* species. While *P. difficilis* was captured more frequently in sampling stations with high presence and coverage of logs in the soil, *P. melanotis* was regularly captured in sampling stations with high vegetation cover and plant species richness. Thus, it seems that the different requirements and habitat preferences of these two *Peromyscus* species facilitate their spatial and temporal coexistence in this mid-latitude temperate forest. In general, we provide evidence of the importance of studying the heterogeneity of the habitat to better understand the interactions between syntopic species, offering new insights into the spatial and temporal mechanisms that could determine its coexistence at local scale.

Un tema fundamental en ecología, es comprender cómo la estructura del hábitat y sus cambios en el espacio y tiempo (*i. e.*, heterogeneidad del hábitat) afectan la frecuencia y las interacciones entre especies que cohabitan. En este estudio, evaluamos el efecto de los componentes bióticos y abióticos que configuran la heterogeneidad del microhábitat y sus cambios temporales (temporada seca y lluviosa), sobre la frecuencia (total y por sexo) de dos especies congenéricas, *Peromyscus difficilis* y *P. melanotis*, que ocurren en un bosque templado del centro de México. Para este fin, una parcela experimental compuesta por 120 estaciones de muestreo fue colocada dentro un bosque templado en el Parque Nacional Desierto de los Leones, Ciudad de México. En cada estación de muestreo, colocamos trampas Sherman para capturar ratones de los dos *Peromyscus* sintópicos, y también evaluamos seis variables relacionadas a la heterogeneidad espacial del hábitat durante dos temporadas lluviosas. Nuestros resultados revelaron efectos diferenciales de la heterogeneidad de hábitat sobre la frecuencia de cada especie. Más aún, la heterogeneidad del hábitat también tuvo un efecto diferente sobre las frecuencias de machos y hembras de cada especie de *Peromyscus*. Mientras que *P. difficilis* fue capturado con mayor frecuencia en estaciones de muestreo con alta presencia y cobertura de troncos en el suelo, *P. melanotis* fue capturado con mayor regularidad en estaciones de muestreo con alta cobertura vegetal y riqueza de especies de plantas. Por lo tanto, parece que los diferentes requerimientos y preferencias de hábitat que tienen estas dos especies de *Peromyscus*, facilitan su coexistencia espacial y temporal en este bosque templado de latitud media. En general, demostramos la importancia de estudiar la heterogeneidad del hábitat para comprender mejor las interacciones entre especies sintópicas, ofreciendo nuevos conocimientos sobre los mecanismos espaciales y temporales que podrían determinar su coexistencia a escala local.

Keywords: Desierto de los Leones; habitat preferences; microhabitat; niche partitioning; small mammals' conservation; species interactions.

Introduction

Co-occurrence processes between different species depend on the spatial scale at which they perceive the habitat (Morris 1987; Barrio and Hik 2013). For instance, it has been proposed that small mammals possibly perceive the habitat structure/heterogeneity at smaller scales than medium-sized or large mammals (*i. e.*, microhabitat; Morris 1984, 1987; Chesson 2000; Whittaker *et al.* 2001). This is relevant since spatial scale may alter species assemblage's patterns perception and the order of importance of the explanatory variables of these patterns (Morris 1987; Whittaker *et al.* 2001). Likewise, coexistence requires species to be different in the way they affect and are affected by competitors and available resources, resulting in niche differences or average fitness differences between species (Chesson 2000; Chen *et al.* 2020). Indeed, differences in the ecological niches occupied by the species within a community act to stabilize the system, with larger differences promoting coexistence (Chen *et al.* 2020). Therefore, determination of the mechanisms for coexistence among several species within a community is of basic ecological interest.

Habitat heterogeneity (*i. e.*, different biotic and abiotic components that shape the habitat architecture) is expected to increase species coexistence of small mammals, as they increase the number of microhabitats that may be occupied by species with different environmental requirements (Rosenzweig and Winakur 1969; Cramer and Willig 2002; Corbalán and Ojeda 2004; Schreiber and Killingback 2013; Novillo *et al.* 2017). Likewise, more available microhabitats offer more shelters for mice to hide from predators, and also provide more diversity of food resources (Corbalán and Ojeda 2004; Traba *et al.* 2010; Novillo *et al.* 2017). However, temporal changes in the habitat structure have also a substantial impact on species coexistence (Valladares *et al.* 2015). For example, changes in the availability of food resources and refuges for species through space and time, affect its population size and how they interact (Valladares *et al.* 2015). Indeed, temporal variation in habitat heterogeneity should increase available niche spaces, allowing more species to coexist (Currie 1991). It has been reported that temporal fluctuations in habitat structure can stabilize species coexistence via the "storage effect" (Chesson 2000), when inter and intra-annual variation in climate or resource availability favors one group of species over others (Zavaleta *et al.* 2003). Similarly, it has reported that the sex of individuals could contribute to the coexistence of two competitive species (Chesson 2000). For instance, it has found a positive effect on coexistence when differences in competitive ability among conspecific individuals (*e. g.*, competition for resources between males *vs.* males or males *vs.* females of the same species) can break down competitive hierarchies of species, such that intraspecific competition is stronger than interspecific competition (Chesson 2000; Hubbell 2005; Fridley *et al.* 2007; Uriarte and Menge 2018).

In this study, we focus on whether different microhabitat elements and their spatial and temporal changes shape the frequency of two syntopic (animals that may use the same habitat; Hart *et al.* 2018) and congeneric species of deer mice (*P. difficilis* and *P. melanotis*). These two model systems were selected for several reasons. First, these two congenerics co-occur in similar habitats and environmental conditions along its distribution (Álvarez-Castañeda 2005; Fernández *et al.* 2010). In the Transmexican Neovolcanic Belt, they cohabit in the understory of mixed and coniferous temperate forests, such as in the Desierto de los Leones National Park (DLNP; Castro-Campillo *et al.* 2008), where this study was conducted. Second, since the DLNP is located at the edge of an ever-growing megalopolis (Mexico City), it is important to understand what elements of the habitat shape the frequency and coexistence of these kind of species to elaborate better strategies to reduce the human impact on natural areas and their wild inhabitants. Urban growth produces fragmentation of natural microhabitats that are important to small mammals, which in turn play a fundamental role in the dispersal of seeds and as habitat architects within the forest.

Third, these two congeneric species have different body sizes (*P. diffilis* is larger than *P. melanotis* (*see* Álvarez-Castañeda 2005; Fernández *et al.* 2010). This morphological differentiation represents an opportunity to compare their different requirements in relation to their respective ecological niche. Four, the reproductive season of *P. difficilis* occurs mainly during the dry season, while that of *P. melanotis* occurs in the rainy season (Castro-Campillo *et al.* 2012; De-la-Cruz *et al.* 2019; Salame-Méndez *et al.* 2018, 2019, 2020). Thus, it is possible that spatial and temporal variation in habitat heterogeneity, such as availability of food resources and shelters, could be related to the different reproductive seasons, relaxing its interspecific competition and promoting its coexistence (Kaufman and Kaufman 1989; Chesson 2000). Nevertheless, while several studies have quantified variation in resource use (*e. g.*, food, shelters, water) in heterogeneous environments among mice from the same genus (Kaufman and Kaufman 1989; Kalcounis-Rüppell and Millar 2002; Villanueva-Hernández *et al.* 2017), there is still a lack of information about how temporal changes in the habitat structure/heterogeneity affect the frequency of congeneric mice species inhabiting at the same place (but *see* Kalcounis-Rüppell and Millar 2002; Hart *et al.* 2018). Here, we measured different variables that compose the structure of the microhabitat and their changes during two rainy seasons (dry and rains), and we related this information with total and sex frequencies of two species of small mammals, *P. difficilis* and *P. melanotis,* that co-occurs in a temperate forest of Central Mexico.

Materials and methods

Study area. The study area (19º18'17"N, 99º19'14"W at 2,289 masl) is located in a mixed temperate forest of coniferous and broad-leaved trees at Desierto de Los Leones National Park (DLNP) in Mexico City (CONANP 2006). This forest is part of the Trans-Mexican Neovolcanic Belt (CONANP 2006). The rainy season occurs from summer through early fall (June to October) with a monthly average precipitation of 252.92 ± 28.01 mm, and an average monthly temperature of 11.72 ± 0.53 °C (CONANP 2006). In contrast, the dry season occurs from fall through winter (October to February); the monthly average precipitation is 13.2 ± 3.11 mm, and the average monthly temperature is 8.97 ± 0.68 (CONANP 2006).

Habitat heterogeneity during dry and rainy seasons. To assess how temporal changes in the habitat heterogeneity affect the frequency of capture of each *Peromyscus* species, we set a plot of 9,900 m² (110 x 90 m; Figures 1a, b). Within this plot, we placed 120 sampling stations every ten meters, along 12 columns (A to L) and ten rows (1 to 10; Figure 1a). Each sampling station was marked with buried wooden stakes. In each sampling station, we delimited an "influence zone" of 2.5 m² (Figure 1b). Within these influence zones of every sampling station, eight fixed transects were set in a clockwise conformation to measure seven variables that qualify as components of the vertical and horizontal struc-

ture of the habitat ([Morris 1984](#); [Jorgensen 2004](#); [Villanueva-Hernández *et al.* 2017](#)). These variables are indicators of possible shelters from predators, spaces for resting and mating, and food resources ([Jorgensen 2004](#)). We applied the Canfield's Line Intercept (CLI) method (Canfield 1941) in each transect of the influence zone to measure the percentage of vegetation coverage at three different heights (10, 35, and 100 cm; VC10, VC35, and VC100, respectively). We also counted the number of all herbaceous plants (H) and the number of all woody plants (W). Likewise, plant species richness (SR) was registered as the number of different plant species found within each influence zone (Figure 1b). The percentage of logs (Logs) covering the ground surface (fallen trees) more than one meter long and ten centimeters in diameter was also registered using Canfield's method. The CLI method is based on the measurement of all plants and objects intercepted by a transect, and the length/coverage of each plant or object that is touched by the line is registered. All habitat features were sampled once during the most representative months of the rainy (July 2017) and dry seasons (February 2018; [CONANP 2006](#)).

Mice trapping. The *Peromyscus* mice were captured alive for ten months to include data for the dry (October 2017 to February 2018) and rainy (March 2018 to July 2018) seasons. We set a single live trap (H. B. Sherman, Inc., Tallahassee, FL 32303, USA), baited with oat flakes and vanilla extract at each sampling station of the plot ($n = 120$). Traps were set for two consecutive nights each month with a total of 20 capture events (10 months x 2 nights; 2,400 night/traps). Mice were marked in their abdomen with gentian violet to avoid overestimation of capture frequencies. Despite this temporal mark did not allow us to identify the mice at individual level (*e. g.*, as with an id code to trace the movements or range home of a certain individual), it turned out to be a practical way to calculate mice abundance accurately by pulling out the recaptured individuals. At the end of the samplings, we could have an estimate of the mice abundance for the dry and rainy seasons. In addition, to avoid recurrence behavior (*e. g.,* mice returning to the traps for bait) or shyness (*e. g.,* mice avoiding traps due to other mice odors), all the traps were thoroughly cleaned and randomly oriented within each sampling station in each capture event. Handling of the mice was following the guidelines of the American Society of Mammalogists ([Sikes 2016](#)). To prevent hypothermia during capture, we placed 3 to 5 cotton balls inside the trap and put the traps inside open plastic bags. We recorded the species and sex of every mouse ([De-la-Cruz *et al.* 2019](#)). If a mouse died overnight while being trapped ($n = 3$), it was skinned and prepared as a study specimen, and incorporated as voucher specimen in the Mammal Collection of the Universidad Autónoma Metropolitana-Iztapalapa. A scientific collecting permit, SEMARNAT–08–049-B, was issued to Alondra Castro-Campillo (ACC) by DGVS, SGPA-09712/13, SEMARNAT, MEXICO.

Statistical analysis. All statistical analyses were performed using the JMP statistical package (v. 14.0; SAS Institute). Plotting was made using ggplot2 ([Wickham 2016](#)) in RStudio version 1.1.463 ([R Core Team 2020](#)).
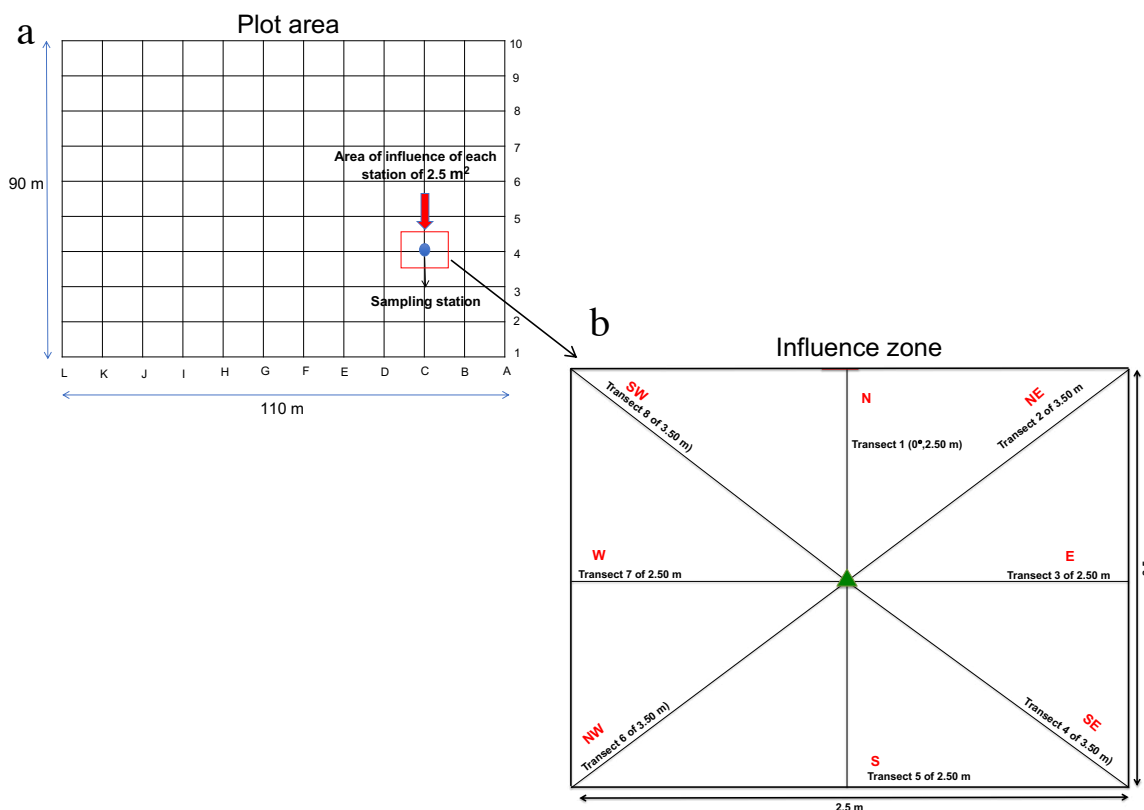

Figure 1. a) Location of the sampling plot in a temperate mixed forest at the Desierto de los Leones National Park, Mexico City. b) Configuration of the experimental plot area (grid) where 120 sampling stations were set with its corresponding influence zone of 2.5 m². Within each influence zone, eight fixed transects were set in a clockwise conformation (North to Southwest) to measure the variables related to the habitat heterogeneity. Green triangle = center of the sampling station where each Sherman trap was also set.

Differentiation of habitat heterogeneity between dry and rainy seasons. Prior to analyses, all variables (habitat elements and mice captures) were log-transformed (log n + 1) to meet normality assumptions. A Student's *t*-test was used to evaluate mean differences between the rainy and dry seasons for each of the seven variables of the habitat heterogeneity (*see* above).

Relationship between habitat heterogeneity and frequency of each Peromyscus species during the dry and rainy seasons. Prior to analyses, variables representing the habitat's heterogeneity and structure were standardized to a mean of zero and a standard deviation of one (X^ = 0, SD = 1). Generalized linear models (GLMs) were used to evaluate the relationships between habitat heterogeneity and the capture frequency of each *Peromyscus* species. All GLMs were performed with 1,000 iterations of the maximum likelihood method. The GLMs described hereafter were selected based on the statistical significance of the model and the lowest corrected AIC values, that is, models that best explained the relationship between the variables ([Akaike 1974](#)).

To evaluate the relationship between the habitat heterogeneity and the frequency of each *Peromyscus*, two GLMs (link = logarithmic, distribution = Poisson) were constructed using the respective abundances of *P. difficilis* and *P. melanotis* as response variables, whereas the vegetation coverage at 10 and 100 cm (VC10 and VC100, respectively), the number of all herbaceous plants (H), the number of all woody plants (W), plant species richness (SR), the percentage of logs (Logs), season, and their interaction were used as predictors. Adding the interaction between season and the covariates in the models, allowed us to assess whether the effect of the habitat heterogeneity or structure differed depending on the season of testing (*cf.* [Zar 1999](#)). A similar GLM was carried out using the abundance of females or males of each *Peromyscus* as response variables.

Since habitat heterogeneity depends on the interaction between different biotic and abiotic elements of the habitat, we also carried out principal component analyses (PCA) for each season, using the seven habitat indicators (variables) to produce new functions that could explain the microhabitat heterogeneity in a more detailed way. Likewise, the PCAs also helped to reduce data dimensionality. One PCA was performed for each season. Since in the dry season, the first two components explained 61.23 % of the variance and in the rainy season, the two first components explained 73.88 % of the variance, we used only these two principal components for subsequent analyses (*see* below).

A GLM (link = logarithmic, distribution = Poisson) was constructed where the response variable was the abundance of *P. difficilis* and/or *P. melanotis* and the two principal components, season and their interaction as covariate effects. A similar GLM was carried out using the abundance of females or males in each *Peromyscus* species as response variables. The generalized linear coefficients (*viz.* βi; [Lande and Arnold 1983](#)) obtained from the GLMs represent the strength and direction of the relationships acting directly on the frequency of the species in comparable units (standard deviations).

Results

Frequency of captures. We captured a total of 516 mice of both *Peromyscus* species for all the study. During the dry season, the total number of captured individuals was 312: 174 individuals for *P. difficilis* (120 males and 54 females) and 138 *P. melanotis* individuals (66, 72). During the rainy season, the total number of captures was 204; 114 individuals of *P. difficilis* (80, 34), and 92 individuals of *P. melanotis* (58, 34).

Changes in habitat structure between the dry and rainy season. The mean difference between seasons was significant for most of the habitat features (Table 1). The mean of almost all habitat variables was higher in the rainy season. Only the coverage of wood logs on the ground surface between seasons did not change (Table 1, Figure 2).

Relationships between frequency of capture for the Peromyscus species and the seven variables of habitat heterogeneity/structure. The GLM between the seven variables that describe the microhabitat heterogeneity/structure and the frequency of *P. difficilis* was significant (*L-R* chi-square$_{15}$ = 37.16, *AICc* = 451.30, *P* = 0.0012, Table 2, Appendix 1). However, only the percentage of logs on the ground (positive effect) and season (positive effect) as predictors were significant. The GLM between the seven habitat variables and *P. difficilis* females' frequency was not significant (*L-R* chi-square$_{15}$ = 15.56, *AICc* = 263.26, *P* = 0.4118, Appendix 1, 2). In this model, the percentage of herbaceous plants (H) showed a significant negative effect on the frequency of females of *P. difficilis*. However, this result must be interpreted with caution. In contrast, the effect of the seven habitat variables on the frequency of males of *P. difficilis* was significant (*L-R* chi-square$_{15}$ = 44, *AICc* = 365.51, *P* = 0.0001, Appendix 1, 2), being percentage of logs covering the ground and the interaction season × woody plants significant predictors (positive effects).

Table 1. Mean (se, standard error) differences in seven elements of microhabitat structure between seasons. VC10 = vegetation coverage at 10 cm, VC35 = vegetation coverage at 35 cm, VC100 = vegetation coverage at 100 cm, H = number of herbaceous plants, W = number of woody plants, SR = plant species richness. d.f. = degrees of freedom. *p* = *p*-values (significant *p*-values are in bold).

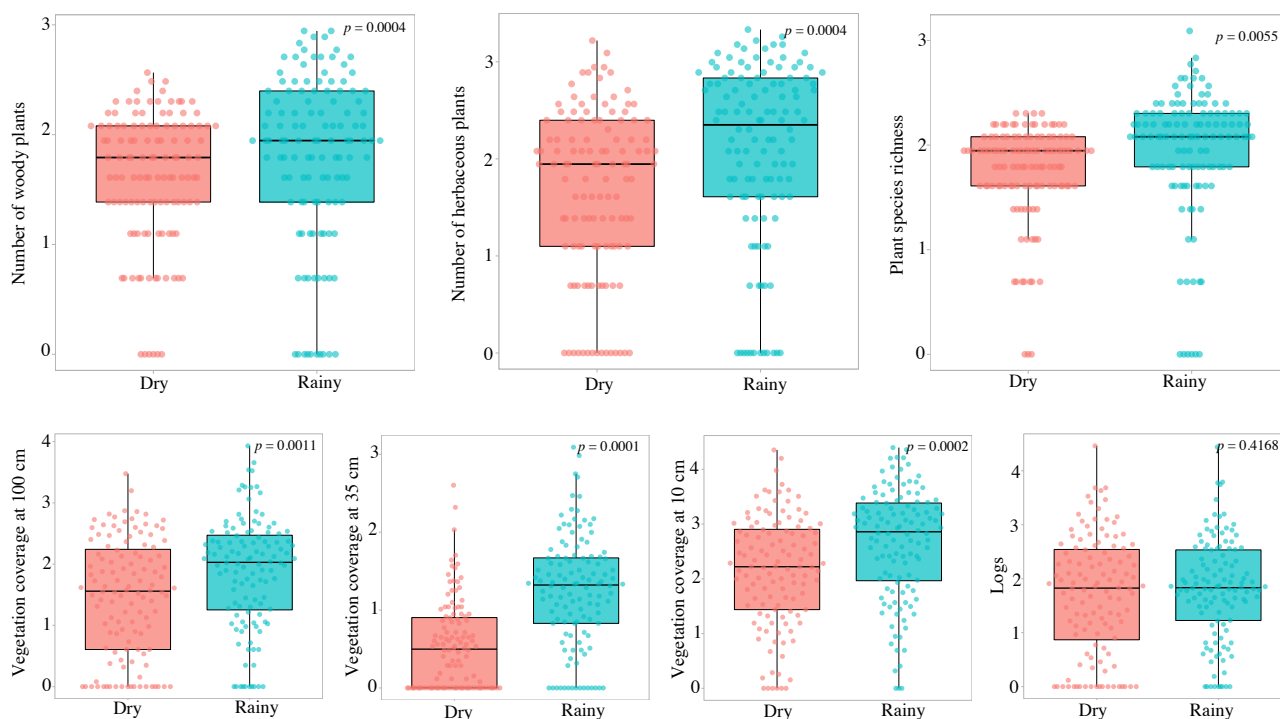| Habitat feature	N	Mean (se)		t	df	p
		Dry season	Rainy season			
VC10	240	12.28 (1.17)	20.10 (1.59)	3.75	238	**0.0002**
VC35	240	1.09 (0.15)	3.44 (0.32)	8.25	238	**0.0001**
VC100	240	5.42 (0.15)	8.28 (0.32)	3.29	238	**0.0011**
Logs	240	8.48 (1.03)	8.37 (0.98)	0.81	238	0.4168
H	240	6.12 (0.47)	9.98 (0.65)	3.60	238	**0.0004**
W	240	4.80 (0.26)	6.55 (0.41)	3.60	238	**0.0004**
SR	240	5.19 (0.19)	7.02 (0.32)	2.80	238	**0.0055**

Figure 2. Median differentiation of the seven variables that describe the habitat heterogeneity between dry and rainy seasons. Dots represent each sampling station. Y-axis is in log scale.

The GLM between the seven variables and the frequency of *P. melanotis* was significant (*L-R* chi-square$_{15}$ = 36.37, *AICc* = 401.37, *P* = 0.0016, Table 2, Appendix 1). Significant effects included the season and plant species richness. Both effects were positively related to the frequency of *P. melanotis*. The GLM between the seven habitat variables and the frequency of *P. melanotis* females was nearly significant (*L-R* chi-square$_{15}$ = 24.93, *AICc* = 277.54, *P* = 0.0508, Appendix 1, 2). In this model, only the season was significant. The effect of the seven habitat variables on the frequency of *P. melanotis* males was significant (*L-R* chi-square$_{15}$ = 34.59, *AICc* = 295.11, *P* = 0.0028, Appendix 1, 2). In this GLM, the effect of the species richness and the interaction between season and species richness were significant and positively related to *P. melanotis* males. On the other hand, the number of woody plants was significant and negatively related to *P. melanotis* males.

Relationships between capture frequency and principal components. Principal component analysis for the dry season showed that the first two components explained almost all the variance (61.23 %). The highest loadings in the first component (PC1) were variables related to vegetation including plant species richness. Hence, this new function describes those sampling stations with high vegetation coverage and species richness. In contrast, the principal component two (PC2) was only related to the coverage of logs on the ground, representing the fixed and stable elements of the habitat. In the rainy season, the first two principal components explained 73.88 % of the variance. As in the dry season, PC1 was related to vegetation and species richness and PC2 with logs' coverage (Appendix 3).

The GLM between the frequency of *P. difficilis* and the principal components was significant (L-R chi-square$_5$ = 30.01, AICc = 436.37; *P* = 0.0001; Table 3, Figure 3 a, b). However, significant predictors only included the PC2, indicating a positive relationship between the frequency of *P. difficilis* and logs' coverage during the two rainy seasons. The GLM between the frequency of *P. difficilis* females and the principal components was not significant (L-R chi-square$_5$ = 3.15, AICc = 253.60; *P* = 0.6767) (Appendix 2). The effect of the principal components on the frequency of *P. difficilis* males was significant (L-R chi-square$_5$ = 36.28, AICc = 351.15; *P* = 0.0001). However, the only significant and positive effect was the PC2 (logs on the ground; Appendix 2).

The GLM between the abundance of *P. melanotis* and the principal components was significant (L-R chi-square$_5$ = 22.46, AICc = 393.20; *P* = 0.0004) (Table 3, Figure 3 c, d). The significant and positive predictors were the PC1 (vegetation) and season in this model. The GLM between the frequency of *P. melanotis* females and the principal components was significant (L-R chi-square$_5$ =12.93, AICc = 267.46; *P* = 0.0240; Appendix 2). The significant effects also included the PC1 and season (positive effects). The GLM between the frequency of *P. melanotis* males and the principal components was also significant (L-R chi-square$_5$ =17.92, AICc = 289.70; *P* = 0.0030; Appendix 2). The significant effects included the PC1 (positive effect) and PC2 (negative effect).

Discussion

Our results revealed different relationships between the habitat heterogeneity and the frequency of both *Peromyscus* species. Likewise, the habitat heterogeneity/structure

Table 2. Effect of the seven microhabitat variables, season (dry, rainy) and their interaction on the frequency of capture of (a) *Peromyscus difficilis* and (b) *Peromyscus melanotis*. d. f. = degrees of freedom, β_i = linear coefficient from the GLM, se = standard error, p = p-value. Significant p-values are in bold. VC10 = vegetation coverage at 10 cm, VC35 = vegetation coverage at 35 cm, VC100 = vegetation coverage at 100 cm, H = number of herbaceous plants, W = number of woody plants, SR = plant species richness.

Response variable (Frequency)	Effects	N	d.f.	β_i	se	L-R ChiSquare	p
Peromyscus difficilis	VC10	240	15	0.02	0.16	0.02	0.8696
	VC35	240	15	0.19	0.11	2.91	0.0876
	VC100	240	15	-0.06	0.13	0.23	0.6262
	H	240	15	-0.26	0.17	2.21	0.1363
	W	240	15	0.08	0.15	0.28	0.5909
	SR	240	15	0.10	0.17	0.36	0.5452
	Logs	240	15	0.24	0.05	13.07	**0.0003**
	Season	240	15	0.23	0.11	4.37	**0.0364**
	Season × VC10	240	15	-0.20	0.16	1.63	0.2012
	Season × VC35	240	15	0.00	0.11	0.00	0.9389
	Season × VC100	240	15	0.09	0.13	0.52	0.4693
	Season × H	240	15	0.19	0.17	1.17	0.2786
	Season × W	240	15	0.27	0.15	3.42	0.0641
	Season × SR	240	15	-0.12	0.17	0.50	0.4768
	Season × Logs	240	15	0.01	0.05	0.04	0.8276
Peromyscus melanotis	VC10	240	15	-0.21	0.17	1.63	0.2013
	VC35	240	15	0.12	0.13	0.83	0.3612
	VC100	240	15	0.15	0.10	1.86	0.1715
	H	240	15	-0.04	0.18	0.05	0.8202
	W	240	15	-0.21	0.16	1.76	0.1844
	SR	240	15	0.53	0.19	7.94	**0.0048**
	Logs	240	15	-0.23	0.14	3.15	0.0758
	Season	240	15	0.40	0.13	9.03	**0.0026**
	Season × VC10	240	15	0.23	0.17	1.89	0.1687
	Season × VC35	240	15	0.03	0.13	0.05	0.8126
	Season × VC100	240	15	-0.07	0.10	0.46	0.4931
	Season × H	240	15	-0.31	0.18	2.92	0.0870
	Season × W	240	15	0.01	0.16	0.01	0.9128
	Season × SR	240	15	0.22	0.19	1.34	0.2467
	Season × Logs	240	15	-0.24	0.14	2.73	0.0981

had a different effect on male and female frequencies of both species of *Peromyscus*. First, while *P. difficilis* was more frequently captured in sampling stations with high presence and coverage of logs on the ground, individuals of *P. melanotis* were usually captured in sampling stations with high vegetation coverage and plant species richness. It has been found that spatial heterogeneity in habitat quality reverses the competition between two sympatric species (Chen *et al.* 2020). Thus, it seems that both *Peromyscus* species have different habitat requirements and preferences that could be facilitating their coexistence in the study zone (Pianka 1973; Chen *et al.* 2020).

Why *P. difficilis* had a higher association in places with a high presence of logs? Logs on the ground surface represent small patches of microhabitat with food sources, burrows and refuges for mice (Bellows *et al.* 2001; Bowman *et al.* 2015; Grelle 2003; Dalmagro and Vieira 2005). Individuals of *P. dif-*

ficilis could also use the large fallen logs as safe pathways for fast and straight locomotion within the forest (Bellows *et al.* 2001; Grelle 2003; Dalmagro and Vieira 2005). Indeed, fallen logs promote the structural heterogeneity of forests and may enhance positive interactions among species of small mammals (Bowman *et al.* 2015). The relationship between *P. difficilis* and microhabitats with a higher number and cover of logs could also be related with the morphology and climbing habits of this species (Fernández *et al.* 2010). For instance, the long tail of *P. difficilis* enables it to rush and climb along shrubs, trees, or logs (Bowman *et al.* 2015), hence, increasing its preference for habitats with fixed elements (*e. g.,* fallen logs), where mice can escape from predators or use holes in logs as burrows (Bowman *et al.* 2015). In contrast, it is possible that *P. melanotis* - the species with smaller body size and more cursorial locomotion - prefers zones with higher vegetation coverage and plant species richness as strategy to

Table 3. Effect of the principal components (PC1-2) as new functions of habitat heterogeneity (*see* methods), season (dry and rainy) and their interaction on the frequency of capture of (a) *Peromyscus difficilis* and (b) *Peromyscus melanotis*. d. f. = degrees of freedom, β_i = linear coefficient from the GLM, se = standard error, p = p-value. Significant p-values are highlighted in bold. VC10 = vegetation coverage at 10 cm, VC35 = vegetation coverage at 35 cm, VC100 = vegetation coverage at 100 cm, H = number of herbaceous plants, W = number of woody plants, SR = plant species richness.

Response variable (Frequency)	Effects	N	d.f.	β_i	se	L-R ChiSquare	p
Peromyscus difficilis	PC1 (Vegetation)	240	5	-0.02	0.04	0.26	0.6084
	PC2 (Logs)	240	5	0.46	0.09	25.65	**0.0001**
	Season	240	5	0.17	0.10	2.97	0.0848
	Season × PC1	240	5	0.02	0.04	0.21	0.6401
	Season × PC2	240	5	-0.00	0.09	0.00	0.9672
Peromyscus melanotis	PC1 (Vegetation)	240	5	0.21	0.06	11.54	**0.0007**
	PC2 (Logs)	240	5	-0.00	0.10	0.00	0.9878
	Season	240	5	0.27	0.11	6.05	**0.0139**
	Season × PC1	240	5	0.00	0.06	0.00	0.9821
	Season × PC2	240	5	-0.19	0.10	3.56	0.0592

avoid predation by aerial hunters or other predators, as well as to obtain food resources more quickly, since seeds may be concentrated under shrub canopies (Bowman *et al.* 2015; Grelle 2003; Dalmagro and Vieira 2005). Likewise, we have found evidence that *P. melanotis* has a higher intermediate metabolism rate than *P. difficilis* (Salame-Méndez and Castro-Campillo, unpublished results). Thus, it is possible that due to its higher metabolic requirements, *P. melanotis* needs to disperse more frequently in search for food resources richer in sugar in areas with higher diversity and richness of plants (such as we observed in this study) that supply its higher metabolic requirements and promoting its ecological niche differentiation (Suarez and Welch 2017; Chen *et al.* 2020).

Our results also revealed that temporal changes in the habitat heterogeneity only seem to affect the frequency of males of both *Peromyscus* species in the study zone, the sex more frequently related to territorial endeavors in mammals (Ostfeld 1990). For instance, males of *P. difficilis* were positively associated with woody plants in the dry and rainy seasons. However, this association was stronger during the dry season. In contrast, males of *P. melanotis* were negatively associated with woody plants in the dry season and positively associated with plant species richness in both seasons, but the association was also stronger during the rainy season. Thus, it seems that there is a different microhabitat use by males of both *Peromyscus* species. Likewise, it is possible that the stronger association between woody plants and males of *P. difficilis* during the dry season could be related to the breeding season of this species. It has been reported that the breeding of *P. difficilis* occurs primarily during the dry season (De-la-Cruz *et al.* 2019; Salame-Mendez *et al.* 2020). Hence, since males could be searching for females to breed during the dry season, it is possible that they are more easily captured than the females or that the density of males in the area increased due to breeding season. This same pattern could also explain the stronger association between males of *P. melanotis* and plant species richness or areas with higher vegetation coverage during the rainy season, where the breeding of *P. melanotis* occurs (De-la-Cruz *et al.* 2019; Salame-Mendez *et al.* 2020).
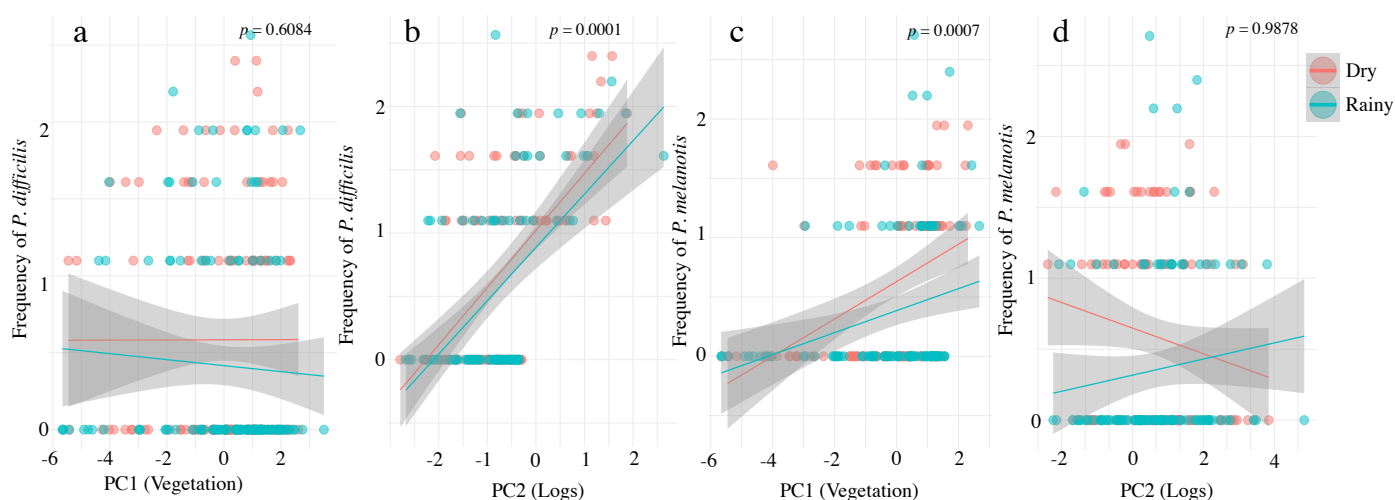

Figure 3. Relationships between the abundance of *Peromyscus difficilis* or *Peromyscus melanotis* with the principal components. p-values are showed in the plots.

Our findings also revealed that females of both *Peromyscus* species did not show a significant association with the microhabitat variables. One explanation is that females may be associated with other habitat variables not measured in this study. Likewise, it is possible that females spend more time in their burrows than males, and they only go out to obtain food and water for short periods, being more cautious and not necessarily associated with a specific habitat component. Indeed, it has been reported for several small mammal species that females have shorter home ranges than males (*e. g.* Ribble et al. 2002; Flores-Manzanero *et al.* 2019). Nevertheless, the lack of a significant association between females and habitat variables could also be related to a statistical bias (Zar 1999), since we captured more males than females during both seasons, except for *P. melanotis* in the dry season where we captured six more females than males of this species.

Finally, this study provides evidence of how two congeneric mice species are affected by the habitat heterogeneity. Interestingly, although these two coexisting *Peromyscus* species can move along different microhabitats (*i. e.*, logs, vegetation coverage), the fact that each one was associated with a different habitat component, suggests a different microhabitat use and selection (Chesson 2000). Habitat partitioning is considered an important mechanism for coexistence among small mammal species (Schoener 1974; Stevens and Tello 2009). Therefore, partitioning of some of the available resources (*e. g.* space, food, refuges, and time) could be enhancing the coexistence of these two syntopic *Peromyscus* species with similar environmental requirements (Shenbrot 1992; Chesson 2000; Novillo *et al.* 2017). Overall, we demonstrate the importance of the study of habitat heterogeneity on the interaction of two syntopic species, offering some new insights into the mechanisms of spatial and temporal coexistence of two mice species at local scale.

Acknowledgments

Literatura citada

Álvarez-Castañeda, S. T. 2005. *Peromyscus melanotis*. Mammalian Species 764: 1–4.

Akaike, H. 1998. A new look at the statistical model identification. Pp. 435, *in* Selected Papers of Hirotugu Akaike (Parzen E., K. Tanabe, and G. Kitagawa, eds.). Springer.

Barrio, I. C., and D. S. Hik. 2013. Good neighbors? determinants of aggregation and segregation among alpine herbivores. **Écoscience 20:276**–282.

Bellows, A. S., J. F. Pagels, and J. C. Mitchell. 2001. Macrohabitat and microhabitat affinities of small mammals in a fragmented landscape on the upper coastal plain of Virginia. The American Midland Naturalist 146:345–360.

Bowman, A. S., J. M. Facelli, and R. Sinclair. 2015. Long-term influence of fallen logs on patch formation and their effects under contrasting grazing regimes. Austral Ecology 40:238–244.

Canfield, R. H. 1941. Application of the line interception method in sampling range vegetation. Journal of Forestry 39: 388–394.

Castro-Campillo, A., A. Salame-Méndez., A. Vergara-Huerta., A. Castillo, and J. Ramírez-Pulido. 2008. Fluctuaciones de micromamíferos terrestres en bosques templados aledaños a la ciudad de México. Pp. 391–410, *in* Avances en el Estudio de los Mamíferos de México (Lorenzo C., E. Espinoza, and J. Ortega, eds.). Publicaciones especiales. Vol. II, Asociación Mexicana de Mastozoología, A. C. Distrito Federal, México.

Castro-Campillo, A., L. León-Altamirano, J. Herrera-Muñoz, I. Salgado-Ugarte, E. Mendienta-Márquez, J. L. Contreras-Montiel, H. Serrano, J. Ramírez-Pulido, and A. Salame-Méndez 2012. Is there a difference between testosterone contents in two populations of the black eared mouse, living under similar conditions but with differences in population patterns? Acta Zoológica Mexicana 28:525-529.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics 31:343–366.

Chen, D., J. Liao, D. Bearup, and Z. Li. 2020. Habitat heterogeneity mediates effects of individual variation on spatial species coexistence. Proceedings of the Royal Society B: Biological Sciences 287(1919):20192436.

Corbalán, V., and R. Ojeda. 2004. Spatial and temporal organization of small mammal communities in the Monte desert, Argentina. Mammalia 68:5–14.

CONANP. 2006. Programa de Conservación y Manejo Parque Nacional Desierto de los Leones. Dirección General de Manejo para la Conservación, Comisión Nacional de Áreas Naturales Protegidas, Secretaría de Medio Ambiente del Gobierno del Distrito Federal, Secretaría del Medio Ambiente y Recursos Naturales. http://www.sma.df.gob.mx/

Cramer, M. J., and M. R. Willig. 2002. Habitat heterogeneity, habitat associations, and rodent species diversity in a sand–shinnery-oak landscape. Journal of Mammalogy 83:743–753.

Currie, D. J. 1991. Energy and large-scale patterns of animal- and plant-species richness. The American Naturalist, 137:27–49.

Dalmagro, A. D., and E. M. Vieira. 2005. Patterns of habitat utilization of small rodents in an area of Araucaria forest in Southern Brazil. Austral Ecology 30:353–362.

De-la-Cruz, I. M., A. Castro-Campillo., A. Zavala-Hurtado., A. Salame-Méndez, and J. Ramírez-Pulido. 2019. Differentiation

pattern in the use of space by males and females of two species of small mammals (*Peromyscus difficilis* and *P. melanotis*) in a temperate forest. Therya 10:3–10.

Fernández, J. A., García-Campusano, F., and M. S. Hafner. 2010. *Peromyscus difficilis* (Rodentia: Cricetidae). Mammalian Species 42:220–229.

Fridley, J. D., Grime, J. P., and M. Bilton. 2007. Genetic identity of interspecific neighbours mediates plant responses to competition and environmental variation in a species-rich grassland. Journal of Ecology 95:908–915.

Flores-Manzanero, A., M. A. Luna-Bárcenas, R. J. Dyer and E. Vázquez-Domínguez. 2019. Functional connectivity and home range inferred at a microgeographic landscape genetics scale in a desert-dwelling rodent. Ecology and Evolution 9:437–453.

Grelle, C. E. V. 2003. Forest structure and vertical stratification of small mammals in a secondary Atlantic forest, southeastern Brazil. Studies on Neotropical Fauna and Environment 38:81–85.

Hart, K. M., A. R. Iverson, I. Fujisaki, M. M. Lamont, D. Bucklin, and D. J. Shaver. 2018. Sympatry or syntopy? Investigating drivers of distribution and co-occurrence for two imperiled sea turtle species in Gulf of Mexico neritic waters. Ecology and Evolution, 8:12656–12669.

Hubbell, S. P. 2005. Neutral theory in community ecology and the hypothesis of functional equivalence. Functional Ecology 19:166–172.

Jorgensen, E. E. 2004. Small mammal's use of microhabitat reviewed. Journal of Mammalogy 85:531–539.

Kalcounis-Rüppell, M. C., and J. S. Millar. 2002. Partitioning of space, food, and time by syntopic *Peromyscus boylii* and *P. californicus*. Journal of Mammalogy 83:614–625.

Kaufman, G. A., and D. W. Kaufman. 1989. An artificial burrow for the study of natural populations of small mammals. Journal of Mammalogy 70:656–659.

Lande, R., and S. J. Arnold. 1983. The measurement of selection on correlated characters. Evolution 37:1210–1226.

Morris, D. W. 1984. Patterns and scale of habitat use in two temperate-zone small mammal faunas. Canadian Journal of Zoology 62:1540–1547.

Morris, D. W. 1987. Ecological scale and habitat use. Ecology 68:362-369.

Novillo, A., M. F. Cuevas., A. A. Ojeda., R. J. A. Ovejero, M. Torres., M. Eugenia., and R. A. Ojeda. 2017. Habitat selection and coexistence in small mammals of the southern Andean foothills (Argentina). Mammal Research 62:219–227.

Ostfeld, R. S. 1990. The ecology of territoriality in small mammals. Trends in Ecology & Evolution, 5: 411–415.

Pianka, E. R. 1973. The structure of lizard communities. Annual Review of Ecology and Systematics 4:53–74.

Platt R. N., B. R. Amman, M. S. Keith, C. W. Thompson, and R. D. Bradley. 2015. What Is *Peromyscus*? Evidence from nuclear and mitochondrial DNA sequences suggests the need for a new classification. Journal of Mammalogy 96:708-719.

R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Ribble, D. O., A. E. Wurtz., E. K. McConnell., J. J. Buegge, and K. C., Jr. Welch. 2002. A comparison of home ranges of two species of *Peromyscus* using trapping and radiotelemetry data. Journal of Mammalogy 83:260–266.

Rosenzweig, M. L., and J. Winakur. 1969. Population ecology of desert rodent communities: habitats and environmental complexity. Ecology 50:558–572.

Salame-Méndez, A., A. Castro-Campillo, H. Serrano, M. D. García-Suárez, J. L., Gómez-Olivares, E. Canchola-Martínez, N. González-Ruiz, and J. Ramírez-Pulido, J. 2018. Annual relation between circulating testosterone and testicular size in adult males of *Peromyscus melanotis* (Rodentia: Cricetidae) in a mid-latitude temperate forest. International Journal of Zoology and Applied Biosciences 3:275-282.

Salame-Mendez, A., A. Castro-Campillo, I. M. De-la-Cruz-Argüello, N. Gonzalez-Ruiz, J. Haro-Castellanos, E. Canchola-Martinez, and J. Ramirez-Pulido, J. 2019. Differential testosterone biosynthesis relates to decoupling of reproductive pattern in *Peromyscus* syntopic species (Rodentia: Muridae). International Journal of Research Studies in Zoology 5:1–7.

Salame-Méndez, A., A. Castro., J. Escobar., J. Vergara-Huerta., H. Serrano., D. García-Suárez., J. A. Haro-Castellanos., N. González-Ruiz., and J. Ramírez-Pulido. 2020. Ecophysiological relationships of environment and reproduction in males of rock mouse (*Peromyscus difficilis felipensis*) at a temperate forest. International Journal of Zoological Research 16:69–78.

Schoener, T. W. 1974. Resource partitioning in ecological communities. Science 185:27-39.

Schreiber, S. J., and T. P. Killingback. 2013. Spatial heterogeneity promotes coexistence of rock–paper–scissors metacommunities. Theoretical Population Biology 86:1–11.

Shenbrot, G. I. 1992. Spatial structure and niche patterns of a rodent community in the south Bukhara desert (Middle Asia). Ecography 15:347–357.

Sikes, R. S. and the Animal Care and Use Committee of the American Society of Mammalogists. 2016. Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. Journal of Mammalogy 97:663–688.

Stevens, R. D., and J. S. Tello. 2009. Micro- and macrohabitat associations in Mojave Desert rodent communities. Journal of Mammalogy, 90:388–403.

Suarez, R. K., and Welch, K. C. 2017. Sugar Metabolism in Hummingbirds and Nectar Bats. Nutrients 9:743.

Traba, J., P. Acebes., V. E. Campos., and S. M. Giannoni. 2010. Habitat selection by two sympatric rodent species in the Monte desert, Argentina. First data for *Eligmodontia moreni* and *Octomys mimax*. Journal of Arid Environments 74:179–185.

Uriarte, M., and Menge, D. 2018. Variation between individuals fosters regional species coexistence. Ecology Letters 21:1496–1504.

Valladares, F., C. C. Bastias, O. Godoy., E. Granda and A. Escudero. 2015. Species coexistence in a changing world. Frontiers in Plant Science, 6.

Villanueva-Hernández, A. I., D. A. Delgado-Zamora., S. A. Heynes-Silerio., L. Ruacho-González., and C. López-González. 2017. Habitat selection by rodents at the transition between the Sierra Madre Occidental and the Mexican Plateau, México. Journal of Mammalogy 98:293–301.

Whittaker, R. J., K. J., Willis, and R. Field. 2001. Scale and species richness: towards a general, hierarchical theory of species diversity. Journal of Biogeography 28:453–470.

Wickham, H. 2016. ggplot2: elegant graphics for data analysis (2nd ed.). Springer International Publishing. New York, U.S.A.

Zar, J. H. 1999. Biostatistical Analysis. Prentice Hall, Princeton. Hoboken, U.S.A.

Zavaleta, E. S., M. R. Shaw., N. R. Chiariello., B. D. Thomas., E. E. Cleland., C. B. Field., and A. H. Mooney. 2003. Grassland responses to three years of elevated temperature, Co_2, precipitation, and N deposition. Ecological Monographs 73:585–604.

Appendix 1

Profilers of the generalized linear models (GLMs) testing the effect of the seven habitat variables on A) total frequency; B) males and females of *Peromyscus difficilis,* and C*)* total frequency; D) males and females of *P. melanotis* during the dry and rainy seasons. VC10 = vegetation coverage at 10 cm. VC35 = vegetation coverage at 35 cm. VC100 = vegetation coverage at 100 cm. H = number of herbaceous plants. W = number of woody plants. SR = plant species richness. Logs = percentage of logs covering the ground.
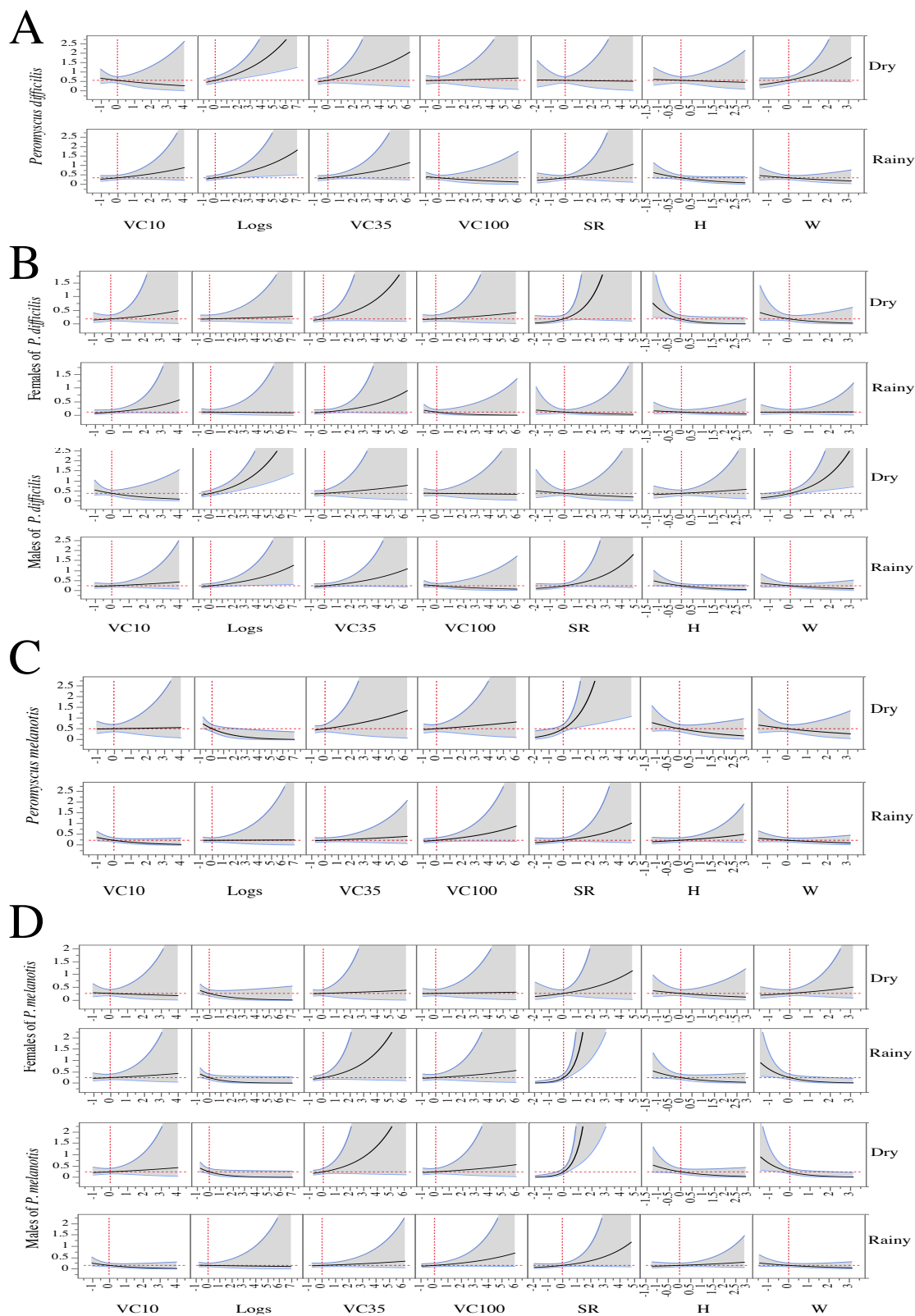
Appendix 2

 Effect of the seven microhabitat variables, seasonality and their interaction on the frequency of (a) females and (b) males of *P. difficilis* and (c) females and (d) males of *P. melanotis.* Effect of the principal components (PC1-2) as new functions of habitat heterogeneity (*see* methods), season (dry and rainy) and their interaction on the frequency of capture of (e) females *Peromyscus difficilis*, (f) males *P. difficilis,* (g) females *P. melanotis* and (h) males *P. melanotis.* d. f. = degrees of freedom, β_i= linear coefficient from the GLM, se = standard error, *p* = *p*-values. Significant *p*-values are in bold. VC10 = vegetation coverage at 10 cm. VC35 = vegetation coverage at 35 cm. VC100 = vegetation coverage at 100 cm. H = number of herbaceous plants. W = number of woody plants. SR = plant species richness. Logs = percentage of logs covering the ground.

Response variable (Frequency)	Effects	n	d.f.	β_i	se	L-R Chi-Square	p
Females of *Peromyscus difficilis*	VC10	240	15	0.30	0.24	1.44	0.2297
	VC35	240	15	0.36	0.17	3.58	0.0584
	VC100	240	15	-0.15	0.24	0.46	0.4940
	H	240	15	-0.70	0.34	4.66	**0.0307**
	W	240	15	-0.27	0.28	0.96	0.3257
	SR	240	15	0.30	0.32	0.85	0.3561
	Logs	240	15	0.01	0.15	0.00	0.9351
	Season	240	15	0.20	0.20	0.98	0.3200
	Season × VC10	240	15	-0.07	0.24	0.08	0.7698
	Season × VC35	240	15	0.03	0.17	0.05	0.8203
	Season × VC100	240	15	0.29	0.24	1.60	0.2045
	Season × H	240	15	-0.44	0.34	1.76	0.1842
	Season × W	240	15	-0.28	0.28	1.04	0.3068
	Season × SR	240	15	0.53	0.32	2.80	0.0941
	Season × Logs	240	15	0.04	0.15	0.08	0.7691
Males of *Peromyscus difficilis*	VC10	240	15	-0.10	0.20	0.27	0.5969
	VC35	240	15	0.18	0.13	1.67	0.1954
	VC100	240	15	-0.11	0.16	0.50	0.4793
	H	240	15	-0.21	0.21	1.06	0.3016
	W	240	15	0.16	0.18	0.81	0.3677
	SR	240	15	0.14	0.20	0.48	0.4856
	Logs	240	15	0.28	0.06	14.25	**0.0002**
	Season	240	15	0.23	0.14	2.79	0.0948
	Season × VC10	240	15	-0.25	0.20	1.59	0.2064
	Season × VC35	240	15	-0.06	0.13	0.24	0.6220
	Season × VC100	240	15	0.09	0.16	0.31	0.5757
	Season × H	240	15	0.36	0.21	2.94	0.0863
	Season × W	240	15	0.47	0.18	7.24	**0.0071**
	Season × SR	240	15	-0.28	0.20	1.89	0.1687
	Season × Logs	240	15	0.04	0.06	0.56	0.4524
Females of *Peromyscus melanotis*	VC10	240	15	-0.40	0.28	2.37	0.1233
	VC35	240	15	0.05	0.18	0.09	0.7627
	VC100	240	15	0.17	0.13	1.46	0.2254
	H	240	15	0.15	0.26	0.34	0.5565
	W	240	15	0.04	0.21	0.04	0.8265
	SR	240	15	0.20	0.26	0.59	0.4395
	Logs	240	15	-0.18	0.19	0.97	0.3235
	Season	240	15	0.56	0.21	7.65	**0.0057**
	Season × VC10	240	15	0.31	0.28	1.22	0.2680
	Season × VC35	240	15	0.00	0.18	0.00	0.9883
	Season × VC100	240	15	-0.14	0.13	1.17	0.2785
	Season × H	240	15	-0.42	0.26	2.55	0.1102

Appendix 2
Continuation

Response variable (Frequency)	Effects	n	d.f.	β_i	se	L-R Chi-Square	p
	Season × W	240	15	0.15	0.21	0.53	0.4652
	Season × SR	240	15	0.10	0.26	0.15	0.6908
	Season × Logs	240	15	-0.27	0.19	1.73	0.1879
Males of *Peromyscus melanotis*	VC10	240	15	-0.17	0.21	0.72	0.3956
	VC35	240	15	0.28	0.16	2.47	0.1160
	VC100	240	15	0.19	0.14	1.63	0.2016
	H	240	15	-0.21	0.24	0.76	0.3822
	W	240	15	-0.63	0.24	7.44	**0.0064**
	SR	240	15	1.03	0.27	15.07	**0.0001**
	Logs	240	15	-0.35	0.20	3.66	0.0556
	Season	240	15	0.21	0.17	1.38	0.2390
	Season × VC10	240	15	0.31	0.21	2.19	0.1381
	Season × VC35	240	15	0.15	0.16	0.83	0.362
	Season × VC100	240	15	-0.05	0.14	0.14	0.7046
	Season × H	240	15	-0.43	0.24	3.23	0.0720
	Season × W	240	15	-0.27	0.24	1.31	0.2523
	Season × SR	240	15	0.61	0.27	5.12	**0.0235**
	Season × Logs	240	15	-0.30	0.20	2.17	0.1405
Females of *Peromyscus difficilis*	PC1	240	5	-0.01	0.07	0.02	0.8694
	PC2	240	5	0.13	0.15	0.82	0.3629
	Season	240	5	0.18	0.15	1.48	0.2226
	Season × PC1	240	5	0.01	0.07	0.01	0.8926
	Season × PC2	240	5	0.08	0.15	0.31	0.5772
Males of *Peromyscus difficilis*	PC1	240	5	-0.04	0.05	0.58	0.4426
	PC2	240	5	0.60	0.10	31.59	**0.0001**
	Season	240	5	0.18	0.12	2.16	0.1414
	Season × PC1	240	5	0.02	0.05	0.24	0.6180
	Season × PC2	240	5	0.01	0.10	0.01	0.9113
Females of *Peromyscus melanotis*	PC1	240	5	0.19	0.10	4.60	**0.0320**
	PC2	240	5	0.06	0.15	0.20	0.6525
	Season	240	5	0.45	0.17	7.89	**0.0049**
	Season × PC1	240	5	-0.06	0.10	0.48	0.4877
	Season × PC2	240	5	-0.17	0.15	1.28	0.2577
Males of *Peromyscus melanotis*	PC1	240	5	0.29	0.09	11.56	**0.0007**
	PC2	240	5	-0.13	0.13	0.98	0.3200
	Season	240	5	0.04	0.15	0.07	0.7886
	Season × PC1	240	5	0.07	0.09	0.66	0.4150
	Season × PC2	240	5	-0.26	0.13	3.99	**0.0456**

Appendix 3

Loadings of the principal components analyses for the dry and rainy season. The highest loadings are marked in red. VC10 = vegetation coverage at 10 cm. VC35 = vegetation coverage at 35 cm. VC100 = vegetation coverage at 100 cm. H = number of herbaceous plants. W = number of woody plants. SR = plant species richness. Logs = percentage of logs covering the ground. % of Variance = percentage of total variance explained by each component.

Dry season	PC1	PC2	PC3	**PC4**	**PC5**	**PC6**	**PC7**
% of Variance	46.8	14.4	12.9	12.0	8.4	3.9	1.6
VC10	0.47	-0.12	0.28	0.20	0.00	0.66	-0.44
VC35	0.25	0.20	-0.76	0.42	0.36	0.01	-0.05
VC100	0.32	0.13	0.07	-0.68	0.63	0.00	0.05
H	0.44	-0.13	0.35	0.40	0.14	-0.18	0.65
W	0.39	0.24	-0.31	-0.34	-0.61	0.25	0.36
SR	0.49	-0.00	0.04	-0.03	-0.25	-0.67	-0.47
Logs	-0.07	0.92	0.33	0.18	0.00	-0.00	-0.06
Rainy season	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**
% of Variance	59.3	14.6	10.0	6.8	5.1	3.0	1.2
VC10	0.41	-0.10	0.05	0.59	0.05	-0.67	0.03
VC35	0.36	0.05	0.62	-0.22	-0.64	0.01	0.04
VC100	0.39	0.01	0.34	-0.44	0.70	-0.07	-0.16
H	0.43	-0.14	0.00	0.36	0.15	0.65	0.44
W	0.36	0.33	-0.54	-0.41	-0.11	-0.22	0.46
SR	0.43	0.19	-0.35	0.09	-0.16	0.24	-0.74
Logs	-0.14	0.90	0.24	0.28	0.13	0.05	0.06